

Article



On the genus *Raphidrilus* Monticelli, 1910 (Polychaeta: Ctenodrilidae) with description of two new species

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Abstract

Raphidrilus harperi sp. nov., is described from the Gulf Intracoastal Waterway (GIWW) in Venice, Florida from sediments consisting of coarse sands and shell hash. Raphidrilus hawaiiensis sp. nov., is described from Oahu's shallow waters and inhabits a successful invasive alga in Waikiki and sandy sediments adjacent to ocean outfalls in Barbers Point and Sand Island, off Honolulu. The genus Raphidrilus is emended, the distinctness between the genera Raricirrus and Raphidrilus is confirmed and keys to all recognized genera of Ctenodrilidae and species of Raphidrilus are given.

Key words: Polychaeta, Ctenodrilidae, Raphidrilus nemasoma, Florida, Hawaii

Introduction

Ctenodrilids are small polychaetes commonly found in soft, shallow—water sediments but some species have been described from the deep sea (Dean 1995) and another only from aquaria (Wilfert 1974). This family currently comprises 2 subfamilies: Ctenodrilinae, which includes those ctenodrilids with a short body, without branchial filaments and reproducing exclusively asexually; and Raphidrilinae for those ctenodrilids with long bodies, branchial filaments present, and reproducing both sexually and asexually (Hartmann—Schröder 1971 emended by Petersen & George 1991).

The distinction of the two genera within the Raphidrilinae, *Raricirrus* Hartman, 1961 and *Raphidrilus* Monticelli, 1910a, was supported by Petersen and George (1991) based on position and extent of the heart body and structure of the nuchal organs. Dean (1995) considered the position of the heart body to be a species level character rather than generic based on variability among species of *Raricirrus* and suggested that the distinctness between *Raricirrus* and *Raphidrilus* are due to the chaetal characteristics and arrangement of prostomium, peristomium and first chaetiger. However, the value of using the presence of modified chaetae in posterior regions as a generic level character was questioned by Dean (1995) based on uncertainties about the posterior end of *Raphidrilus* because no specimens of *Raphidrilus nemasoma* Monticelli, 1910a had been carefully examined. The relationships within the Raphidrilinae remained unclear.

Descriptions of two new species of *Raphidrilus* from Venice, Florida and the south shore of Oahu, Hawaii are presented, including notes on the external morphology of anterior fragments of the type species *Raphidrilus nemasoma* based on newly collected material from the northern Adriatic Sea. The genus *Raphidrilus* is emended and the separation between *Raricirrus* and *Raphidrilus* is maintained. Keys to all recognized genera of Ctenodrilidae and species of *Raphidrilus* are presented.

Material and methods

Several fragmented specimens of *Raphidrilus nemasoma* were collected from the thallus of *Caulerpa racemosa*, an invasive alga growing on soft bottoms in the northern Adriatic Sea, by SCUBA diving. The alga canopy was

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removed using scissors and fixed in the laboratory in 4% buffered formaldehyde–seawater solution. Worms were sorted from the debris and preserved in 70% ethanol.

Several complete and incomplete specimens of *Raphidrilus harperi* sp. nov., were identified from sediment samples collected in the Gulf Intracoastal Waterway (GIWW) at Venice, Florida, USA. This area of the canal is tidally influenced and bordered by banks of armour rocks. The sample location was located 152 meters north and 14 meters west of an outfall from a reverse osmosis plant. Sediments at this site consist mostly of coarse sands and shell hash. Sediment samples were fixed with 10% buffered formalin and preserved in 70% ethanol. Water quality measurements were also taken.

Several complete, incomplete, and regenerating fragments of *Raphidrilus hawaiiensis* **sp. nov.**, were collected from beds of the invasive alga *Gracilaria salicornia* in reefs adjacent to the Natatorium in Waikiki, Oahu, Hawaii, USA. Other specimens were collected from reef flats near the Paiko Lagoon Sanctuary, south coast of Oahu, from the branches of the chlorophyte alga *Avrainvillea amadelpha* and also from sewage outfall sediment samples taken from reference stations close to the Sand Island and Barbers Point outfall diffusers, south coast of Oahu. All samples were fixed in a buffered formalin and Rose Bengal mixture, elutriated over a 0.5 mm sieve, sorted, and preserved in 70% ethanol.

Individuals of *Raphidrilus harperi* **sp. nov.**, *R. hawaiiensis* **sp. nov.**, and *R. nemasoma* were placed in a nitric acid bath for 24 hours following the acid dissolution technique modified from the methods of Brock and Brock (1977) (as described in Nelson 1986). The acid bath helps to dissolve the fine sediment coating usually present over the worm's surface. For Scanning Electron Microscopy (SEM) analysis, the worms were dehydrated through a series of increasing concentration of ethanol ending with 2 changes of absolute ethanol followed by critical point drying using a SAMDRI–795. Specimens were then mounted on stubs and coated with gold/palladium for 2 minutes at 5 nm. SEM observations were carried out using the Hitachi S–4800 at the Biological Electron Microscopy Facility (BEMF), University of Hawaii at Manoa.

Type material of *Raphidrilus harperi* **sp. nov.**, *R. hawaiiensis* **sp. nov.**, and voucher specimens of *R. nemasoma* were deposited in the following museums:

BMNH British Museum of Natural History, London, UK

BPBM Bernice Pauahi Bishop Museum, Honolulu, Hawaii, USA

FSBC I Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute Inverte-

brate Specimen Collection, St. Petersburg, Florida, USA

MAGNT Museum and Art Gallery of the Northern Territory, Darwin, Australia

USNM United States National Museum of Natural History, Smithsonian Institution, Washington, D. C., USA

Additional non-type material for *Raphidrilus harperi* **sp. nov.**, is located in the third author's personal collection and for *R. hawaiiensis* **sp. nov.**, in the Wormlab's reference collection, Department of Zoology, University of Hawaii at Manoa, Hawaii, USA.

Taxonomic account

Family Ctenodrilidae Kennel, 1882

Subfamily Raphidrilinae Hartmann-Schröder, 1971

Genus Raphidrilus Monticelli, 1910a

Type species: Raphidrilus nemasoma Monticelli, 1910a

Type locality. Gulf of Naples in the Mediterranean Sea.

Diagnosis (emended after Monticelli, 1910a). Raphidrilinae with peristomium obviously delimited from prostomium and first achaetous segment both dorsally and ventrally; nuchal organs shallow depressions with cilia; 1–2 dorsally biannulated achaetous segments between peristomium and first chaetiger; posterior end indistinct

from posterior segments. Heart body always present from chaetiger 4. Serrate capillaries throughout; more abundant anteriorly. Reproduction sexual and asexual.

Remarks. The presence of at least one dorsally biannulated achaetous segment between the peristomium and chaetiger 1 is constant in R. harperi sp. nov., R. hawaiiensis sp. nov., and R. nemasoma, and has not been described from other ctenodrilid species.

Dean (1995) points out that the origin of the heart body should not be used as a diagnostic character for the genera Raphidrilus and Raricirrus, because in Raricirrus variabilis it begins at chaetiger 4 (4-6) as well as in all Raphidrilus species. The position and extent of the heart body in the three described species of Raphidrilus seems to be a species level character given that the heart body begins at chaetiger 4 in all three but differs in how the heart body projects anteriorly or posteriorly to one or more chaetigers.

Monticelli's description of Raphidrilus nemasoma reports a male phase with distinctive smooth curved spines in segments 5-8. All incomplete specimens from the Mediterranean that were examined under SEM do not bear such spines. Petersen and George (1991) pointed out that the possible undescribed Raphidrilus described by Qian and Chia (1989) as having short genital spines, may in fact have normal neurochaetae. Because such genital spines have not been found in any specimen examined of R. harperi sp. nov., or R. hawaiiensis sp. nov., we believe this feature should be species specific (if truly present), rather than being generic in diagnosis.

The morphological characters useful in differentiating species within the genus Raphidrilus, not in order of importance, are: 1) Shape of prostomium; 2) Presence/distribution of short sensory cilia in addition to the nuchal organs on the prostomium; 3) Number of dorsally biannulated anterior achaetous segments; 4) Shape of thoracic and abdominal segments; 5) Position and extent of the heart body; 6) General shape of the digestive tube; 7) Presence of sensorial tufts on parapodia (Qian & Chia 1989); 8) Number, length and distribution throughout the body of the capillary chaetae; 9) Arrangement of the capillary fibrils seen under SEM; and 10) Position of the anal aperture and presence of fields of cilia.

Key to genera of Ctenodrilidae (After Petersen & George 1991 and Dean 1995)

1A	With long bodies (up to c. 35 segments); with filamentous branchiae (subfamily Raphidrilinae)
1B	With short bodies (up to c. 15 segments); without branchiae (subfamily Ctenodrilinae)
2A	Anterior segments distinct dorsally; 1–2 anterior and dorsally biannulate achaetous segments; indistinct posterior end; serrated
	capillaries throughout
2B	Anterior segments indistinct dorsally; distinct posterior end with 1–2 modified posterior segments; chaetae may include serrate
	and coarsely serrate capillaries, pectinate falcigers, and simple curved spines
3A	All chaetae coarsely serrate
3B	With capillaries in addition to serrate forms

Key to species of *Raphidrilus* (After Monticelli, 1910b)

1A	Prostomium with a pair of nuchal organs only; parapodia without sensorial tufts; dorsal anal aperture
1B	Prostomium with scattered sensorial tufts in addition to a pair of nuchal organs; parapodia with sensorial tufts; terminal anal
	aperture
2A	Three to six capillaries in thoracic chaetigers; abdominal chaetigers 1.5–4 times longer than wide and without sub–annulations;
	heart body extends posteriorly more than one chaetiger
2B	No more than four capillaries in thoracic chaetigers; abdominal chaetigers 1–2 times as long as wide; heart body extends ante-
	riorly or restricted to one chaetiger
3A	One or two dorsally biannulated anterior achaetous segment; heart body anteriorly directed to the middle of chaetiger 3; dis-
	tance between the insertion point of two capillary fibrils along the capillary chaetae approximately the same as half the width
	of a single fibril
3B	Only one dorsally biannulated anterior achaetous segment; heart body restricted to chaetiger 4; distance between the insertion
	point of two capillary fibrils along the capillary chaetae approximately the same as the width of a single fibril

Raphidrilus nemasoma Monticelli, 1910a

Figure 1 (A–D)

Raphidrilus nemasoma Monticelli, 1910a: p. 61-64.

Raphidrilus nemasoma; Monticelli, 1910b: p. 403–406, pls. 12–13; Banse, 1959a: p. 307; possibly Banse, 1959b: p. 170–171, fig. 2; possibly Bellan, 1964; not Harris, 1971: p. 706, fig. 14; Katzmann, 1972: p. 136; not Qian & Chia, 1989: p. 2350, figs. 1–18.

Ctenodrilus branchiatus Sokolow, 1911a: p. 548–565, plates XXVII–XXIX.

Material examined. Croatia: Vrsar Harbor, northern Adriatic Sea, 45°08,989′ N 13°35,776′ E, collected from the thallus of *Caulerpa racemosa* (Forsskål) J. Agardh, coll. Barbara Mikac, 08/12/2008 (9 anterior fragments mounted on stub, USNM 1150464).

Description. Small and incomplete specimens, 1–2.5 mm long, 0.05–0.1 mm wide with 5–11 anterior chaetigers. First four chaetigers (thorax) wider than long; abdominal chaetigers twice longer than wide with sub–annulations

Prostomium short, broadly round; peristomium single achaetous annulation followed by one dorsally biannulated achaetous segment (Fig. 1A, B). Parapodia with serrated capillaries throughout (Fig. 1C, D). Anterior chaetigers with 4 serrated capillaries in each noto— and neuropodia; number of chaetae reduces from chaetiger 5–6 to 1–2 serrated capillaries in posterior chaetigers. Distance between the insertion point of two capillary fibrils along the capillary chaetae approximately the same as the width of a single fibril (Fig. 1C, D). Branchial filaments arising posterodorsal to notochaetae. Posterior end and pygidium not observed.

Distribution. *Raphidrilus nemasoma* seems to be widely distributed in the Ligurian and Tyrrhenian seas (Castelli *et al.* 1995) and the northern Adriatic Sea.

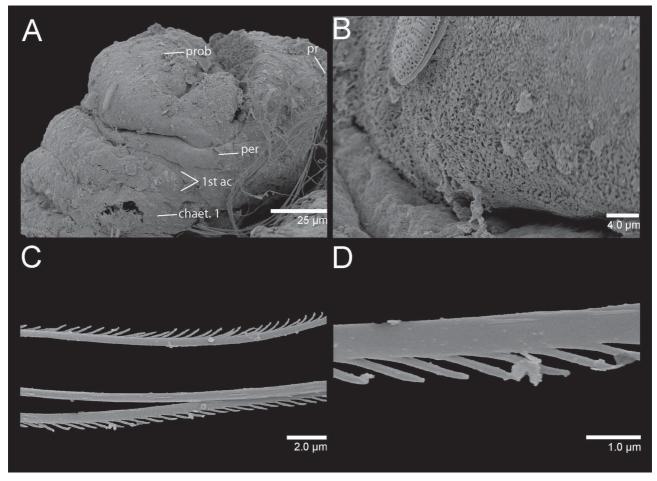


FIGURE 1. SEM of *Raphidrilus nemasoma* showing: A, anterior end in lateral view; B, base of ventral proboscis; C, D, serrate capillaries.

Remarks. The specimens analyzed from the northern Adriatic Sea agree well with the description of *R. nemasoma* by Monticelli (1910a, b). Monticelli (1910b) reported an achaetous segment before chaetiger 1, but referred to it as the peristomium; however, SEM analysis of *R. nemasoma* specimens newly collected showed an additional achaetous segment posterior to the peristomium. The dorsal distinction between prostomium and peristomium, however, is not easily seen using light microscopy, even at 1000x magnification.

The type series of *R. nemasoma* are believed to be lost or never kept (see discussion in Petersen & George 1991) but the specimens newly collected from the northern Adriatic Sea are not well enough preserved to be assigned as neotypes and were not collected near the type locality (Naples Gulf, Italy). More complete and well preserved specimens are necessary to better assess the external morphology of this species, even though detailed descriptions of the external morphology and internal anatomy are available in Monticelli (1910b) and Sokolow (1911a).

Raphidrilus harperi sp. nov.

Figures 2 (A–C) and 3 (A–F)

Material examined. Holotype: GIWW at Venice, Florida, USA, 27°06'01.3" N, 82°26'08.5" W, Station 5NB, coll. D. Seagle, August 28, 2009 (USNM 1150467). **Paratypes:** same location, date and collector as holotype, Station 5NB (9, USNM 1150469); Stations 5NB and 5NC (4, FSBC I 072250); Station 5NB (4, MAGNT W23467–W23470); Station 5NB (1 mounted on stub, BMNH 2011.7); Station 5NB (2 mounted on stub, USNM 1150468). **Non-type material:** same location, date and collector as type-series, Station 5NB (3); Station 5NC (1).

Description. Complete specimens ranged from 3.1–5.8 mm in length, 0.1–0.25 mm in width and possessed between 17–27 chaetigers. Body thin, cylindrical, and elongated. First four chaetigers (thorax) and last few wider than long; abdominal chaetigers vary from 1.5–4 times longer than wide (Fig. 2A). Color in alcohol light yellow to brown.

Prostomium short, broadly rounded with pair of postero–lateral nuchal organs (Fig. 3C). Nuchal organs oval ciliary patches (\sim 7 μ m) with long cilia, situated in a shallow depression (Fig. 3D). Distinction between prostomium and peristomium inconspicuous laterally; peristomium single achaetous segment, appearing pear–shaped together with the prostomium; a single biannulated achaetous segment following the peristomium (Fig. 3B). Heart body usually begins in chaetiger 4, but sometimes projects anteriorly into the posterior region of chaetiger 3; usually extends to chaetiger 7, but occasionally continues to chaetiger 9 in the material examined (Fig. 2A). Branchial filaments postero–dorsal to notochaetae, easily broken and occurring in pairs or singly from chaetigers 3 through 11 (Fig. 3A, B).

Anterior chaetigers with 3–6 serrated capillaries in both noto– and neurochaetal fascicles; posterior chaetigers with 1–4 capillaries per fascicle. Serrations of some capillaries evident using phase contrast microscopy with oil immersion at 1000x magnification; SEM revealed fibrils along capillary edge with distance between the insertion point of two capillary fibrils approximately the same as half the width of a single fibril (Fig. 3E).

Pygidium elongated segment with dorsal anal aperture; fields of cilia not observed (Fig. 3F).

Etymology. This species is named in honor of the third author's graduate advisor, Dr. Donald E. Harper, Jr., Professor Emeritus of Texas A&M University at Galveston. Dr. Harper graciously introduced me to the world of polychaetes and has provided valuable guidance and encouragement over the years.

Biology. Raphidrilus harperi **sp. nov.**, was collected just north of a reverse osmosis plant outfall. Water quality data is typical for a shallow, estuarine waterbody during late summer in southwest Florida (Table 1). All specimens were sexually immature and regenerating specimens were not observed. Segmented worms were observed, however, in the coelom of several specimens and were oriented in both directions along the anterior–posterior axis of the host (Fig. 2B, C). Segmented worms were dissected out of the host and neither chaetae nor branchiae were observed. These segmented worms may be an intracoelomic parasite or gestational larvae resulting from sexual reproduction. Petersen and George (1991) indicated protandric hermaphroditism with internal gestation for *R. nemasoma*. Additionally, Sokolow (1911a, fig. 77) illustrated juveniles emerging from the coelom of a parent, which appear quite similar to the segmented worms observed in *R. harperi* **sp. nov.** (Fig. 2A–C). Future *in vivo* investigations would help resolve the unknown reproductive processes of *R. harperi* **sp. nov.**

TABLE 1. Bottom water quality parameters for the sampling station where *Raphidrilus harperi* **sp. nov.**, and *R. nemasoma* were collected.

Species	Depth (m)	Water Temperature (°C)	Salinity (ppt)	Dissolved Oxygen (mg/L)	Specific Conductivity (µmho/cm)	рН	Chlorides (g/ Kg)
R. harperi sp. nov.	2.7	30.0	26.1	3.58	40,600	7.3	14.4
R. nemasoma	6.4	14.0	37.725	_	_	_	_

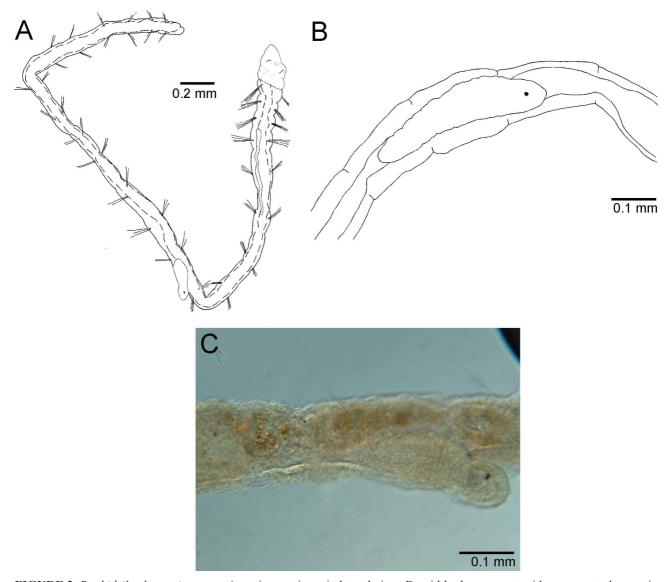


FIGURE 2. Raphidrilus harperi **sp. nov.** A, entire specimen in lateral view; B, mid-body segments with a segmented worm in the coelom; C, light microscopy of mid-body segments showing a segmented worm protruding from the coelom.

Distribution. Raphidrilus harperi **sp. nov.**, is known only from the type locality, the GIWW in Venice, Florida. The distribution of this species is suspected to extend further south into the Florida Keys (T. H. Perkins, pers. comm.) if it is the same species that Petersen and George (1991) referred to in their study. Unfortunately, those specimens have been lost (T. H. Perkins, pers. comm.), and could not be observed for comparison. Based upon correspondence and associated drawings between T. H. Perkins and M. E. Petersen specimens from the Florida Keys superficially appear to be *R. harperi* **sp. nov.** The general body shape, number of chaetae per fascicle and the description of chaetae all match *R. harperi* **sp. nov.** The only difference is that no branchiae or scars of branchiae were observed in the specimens from the Florida Keys, whereas almost all specimens from Venice have at least a stub, a single branchial filament or multiple branchial filaments. Additional specimens from the FSBC I collections labeled as "Raphidrilus sp." were examined for comparison (FSBC I 45229 and FSBC I 45230). These specimens

were collected from Broward County along the east coast of Florida and are not *R. harperi* **sp. nov.** They possess pectinate falcigers in the middle and posterior chaetigers and are most likely an undescribed species of *Raricirrus*. Future collection efforts along the Gulf coast of Florida would help determine the geographical distribution of *R. harperi* **sp. nov.**

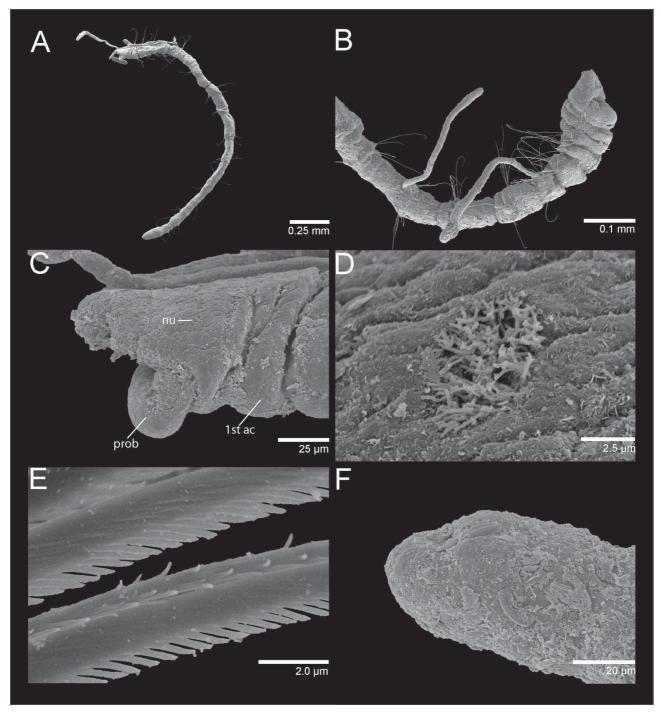


FIGURE 3. SEM of *Raphidrilus harperi* **sp. nov.** showing: A, complete specimen; B, anterior chaetigers in lateral view with two branchial filaments; C, anterior segments in lateral view; D, nuchal organ; E, serrate capillaries; F, pygidium.

Remarks. Table 2 summarizes the morphological characters useful to separate species in the genus *Raphidrilus*. *Raphidrilus harperi* **sp. nov.**, differs from *R. hawaiiensis* **sp. nov.**, and *R. nemasoma* by the presence of 3–6 capillary chaetae per fascicle in anterior chaetigers, while in both *R. hawaiiensis* **sp. nov.**, and *R. nemasoma* the number of capillaries per fascicle is never greater than 4. The elongated mid–body and posterior segments in *R. harperi* **sp. nov.**, is also very distinct and lack sub–annulations present in *R. hawaiiensis* **sp. nov.**, and *R. nem-*

asoma. The heart body in *R. harperi* **sp. nov.**, extends posteriorly to chaetigers 7–9, while in *R. hawaiiensis* **sp. nov.**, the heart body projects anteriorly to the middle of chaetiger 3 and in *R. nemasoma* the heart body is restricted to the extension of chaetiger 4 (Monticelli 1910b).

The species of *Raphidrilus* referred to by Qian and Chia (1989) as *Raphidrilus nemasoma*, and later considered to be undescribed by Petersen and George (1991), is distinct from *R. harperi* **sp. nov.**, *R. hawaiiensis* **sp. nov.**, and *R. nemasoma*. Even though adult worms of *Raphidrilus* sensu Qian and Chia (1989) were not described by these authors, the many scattered short sensory cilia in addition to the nuchal organs present on the prostomium and peristomium, the sensory tufts postero–dorsal to notochaetae, the short serrate neurochaetae (reported as being genital spines), and the terminal anus of juveniles worms (8–11 chaetigers) are unique characteristics not observed in the species from Florida, Hawaii, or the Mediterranean Sea. Adult specimens from the same locality sampled by Qian and Chia (1989) need to be examined to confirm the status of a new species.

TABLE 2. Taxonomic characters of four *Raphidrilus* species including one undescribed species from the western Pacific.

Species	Prostomium	Peristomium	Achaetous segment	Position and extent of heart body
R. harperi sp. nov.	Rounded; pair of oval nuchal organs; pear–shaped with peristomium	Single annulus; not dor- sally delimited from pros- tomium	One dorsally biannulated	Chaetiger 4; posteriorly directed to chaetiger 7
R. hawaiiensis sp. nov.	Rounded; pair of oval nuchal organs; pear–shaped with peristomium	Single annulus; not dorsally delimited from prostomium	1–2 dorsally biannulated	Chaetiger 4; anteriorly directed to middle of chaetiger 3
R. nemasoma Monticelli, 1910	Broadly rounded; a pair of nuchal organs; thimble–shaped with peristomium	Single annulus; not dorsally delimited from prostomium	One dorsally biannulated	Chaetiger 4 only
R. sp. sensu Qian & Chia, 1989*	Broadly rounded; a pair of nuchal organs and scattered sen- sorial tufts; thimble–shaped with peristomium	Single annulus?	One dorsally biannulated?	?

^{*} based on juveniles with 8–11 chaetigers. continued.

Species	Thoracic chaetigers	Abdominal chaetigers	Pygidium	Reproduction
R. harperi sp. nov.	Chaetigers 1–4 wider than long with 3–6 capillaries in each fascicle	From chaetiger 5, chaetigers 1.5–4 times longer than wide, without subannulations; number of capillaries reduce to 1–4 per fascicle	Elongated segment; dorsal anal aperture; fields of cilia not observed	Sexual (with internal gestation? See Figures 2B, C); Asexual reproduction not observed
R. hawaiiensis sp. nov.	Chaetigers 1–4 wider than long with 4 cap- illaries in each fasci- cle	From chaetiger 5, chaetigers as long as wide, with sub–annulations; number of capillaries reduce to 1–2 per fascicle	Elongated segment; dorsal anal aperture; fields of cilia present	Sexual (with internal gestation? See Figure 4C) and asexual (architomic scissiparity)
R. nemasoma Monticelli, 1910	Chaetigers 1–4 wider than long with 4 cap- illaries in each fasci- cle	From chaetiger 5, chaetigers twice longer than wide, with sub–annulations; number of capillaries reduce to 1–2 per fascicle	Elongated segment; dorsal anal aperture; fields of cilia not observed	Sexual (protandric her- maphrodite with internal gestation) and asexual (architomic scissiparity)
R. sp. sensu Qian & Chia, 1989	Chaetigers 1–4 wider than long with 4 cap- illaries in each fasci- cle; neuropodial capillaries shorter than notopodial ones; parapodia with senso- rial tufts	From chaetiger 5, chaetigers twice longer than wide; neuropodial capillaries shorter than notopodial ones; parapodia with sensorial tufts	Elongated segment; terminal anus; fields of cilia present	Sexual (gonochoristic with external gestation; eggs laid in a jelly mass). Asexual reproduction not reported

Material examined. Holotype: Kaimana Beach, Waikiki, south shore of Oahu, Hawaii, 21°15′45″ 157°49′19″, collected from mud adhering to branches of the brown alga *Gracilaria salicornia* (C. Agardh), coll. W. Magalhães, Oct/09 (USNM 1150465); Paratypes: same location, date and collector as holotype (8, BPBM-R3434; 5, USNM 1150466; 5, BMNH 2011.2–6). Non–type material: Kaimana Beach, Waikiki, Oahu, Hawaii, on *Gracilaria salicornia* 21°15′50″ 157°49′21″, coll. C. Moody, Jan/09 (42); July/2008 (8); coll. W. Magalhães, Oct/09 (10); Sand Island outfall, off Honolulu, Oahu, Hawaii, station D6R1, 2004, 50 m (9); Barbers Point outfall, off Honolulu, Oahu, Hawaii, 66 m, station HB1R5, 2004 (6), station HB3R5, Jan/10 (1); Sand beach 1000 m west from Paiko Lagoon Sanctuary, south shore of Oahu, Hawaii, 21°16′47″ 157°43′45″, collected on *Avrainvillea amadelpha* (Mont.) A. Gepp & E. Gepp, station A7R3, coll. W. Magalhães, Mar/10 (4).

Description. Specimens 2–3 mm long, 0.1–0.2 mm wide for 12–26 chaetigers. Body elongated, cylindrical, and indistinct posteriorly (Fig. 4A). First four chaetigers (thorax) and last few wider than long (Figs. 4A; 5F); abdominal chaetigers as long as wide, sometimes sub–moniliform. From chaetiger 5 to posterior end 10–20 sub–annulations present per segment (Fig. 6B). Branchiae scarce in adults, frequently broken off, present on variable number of anterior chaetigers. Color in alcohol light yellow; few specimens yellow to dark brown; internal structures observed through transparent body wall. Color in life not observed.

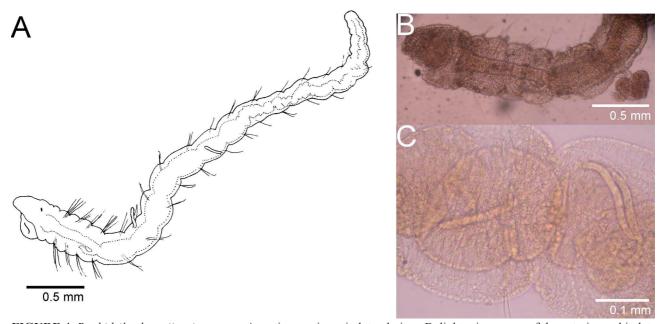


FIGURE 4. *Raphidrilus hawaiiensis* **sp. nov.** A, entire specimen in lateral view; B, light microscopy of the anterior end in lateral view; C, light microscopy of mid-body chaetigers showing intracoelomic worms.

Prostomium as long as two anterior chaetigers, pear–shaped, with pair of nuchal organs located near postero–lateral border (Fig. 5A–C). Nuchal organs oval ciliary patches (8–10 µm wide) with long cilia, situated in a shallow pit (2–3 µm deep) (Fig. 5D). Peristomium consisting of single achaetous segment not clearly distinct dorsally from prostomium (Fig. 5A–C); ventral proboscis with numerous basal bar–like papillae (Fig. 5E). One (N=38) or two (N=5) achaetous segments biannulated dorsally; one specimen with three achaetous segments but third one not biannulated. First four chaetigers short, with 4 notochaetae and 4 neurochaetae in each fascicle; subsequent chaetigers with 1–2 chaetae per fascicle. Heart body always on chaetiger 4; sac–like, anteriorly directed, extending to middle of chaetiger 3 (Fig. 4B). Digestive tube divided in three parts; cylindrical esophagus enlarges at chaetiger 5 in all specimens where inflated stomach begins (Fig. 4A, B); posterior third of the body with curled digestive tube (Fig. 4A); number of segments with inflated stomach and curled intestine variable.

Branchial filaments postero—dorsal to notochaetae (Fig. 6A). Serrate capillary chaetae throughout (Fig. 6C, D), emerging directly from the body wall (Fig. 6A). Chaetae few or absent on far posterior chaetigers. Fibrils along the capillary edge with distance between the insertion point of two capillary fibrils approximately the same as half the width of a single fibril.

Anal aperture dorsal on elongated pygidial segment, covered by fields of long cilia (Fig. 6E, F).

Biology. Raphidrilus hawaiiensis **sp. nov.**, is usually found in low abundance (10–70 ind./m², Ambrose *et al.* 2010) adjacent to ocean outfalls in sandy bottoms and in high abundance (1125 ind./m², C. Moody, unpublished data) on the invasive alga *Gracilaria salicornia*, which is a successful invader on Oahu's south shore reef flats. Few specimens were found inhabiting branches of the green invasive alga *Avrainvillea amadelpha. Raphidrilus hawaiiensis* **sp. nov.**, has been collected with a fine sediment coating of unknown function, but this sediment coat (mostly composed of fragments of diatoms, radiolarians, and clay particles) may protect the worms against the adhesive properties of algal mucilage and abrasion.

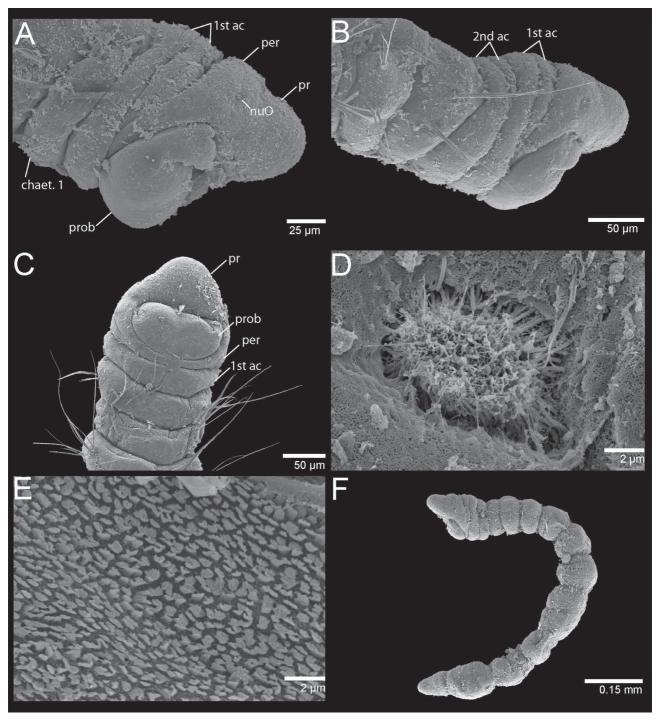


FIGURE 5. SEM of *Raphidrilus hawaiiensis* **sp. nov.** showing: A, anterior end in lateral view of a worm with 1 achaetous segment; B, anterior end in lateral view of a worm with 2 achaetous segments; C, anterior end in ventral view; D, nuchal organ, E, proboscideal papillae, F, juvenile individual.

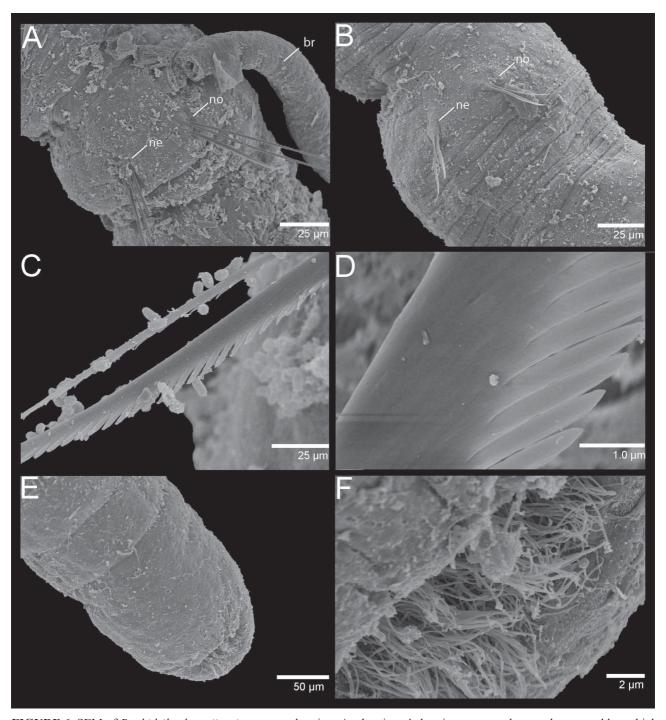


FIGURE 6. SEM of *Raphidrilus hawaiiensis* **sp. nov.** showing: A, chaetiger 4 showing noto— and neurochaetae and branchial insertion; B, mid–body chaetiger with sub–annulations; C, D, serrate capillaries; E, posterior end and pygidium in dorsal view; F, pygidial cilia.

Raphidrilus hawaiiensis sp. nov., reproduces asexually and maybe sexually. Some specimens, even one regenerating fragment (Fig. 7F), had what may be larvae in the coelom, but no larval chaetae or segmentation were observed, so this might be intracoelomic parasites (Fig. 4C). If these small worm-like individuals are indeed larvae, it might indicate that this species is a viviparous hermaphrodite with larvae exiting the body as juvenile worms as reported for *R. nemasoma* (Monticelli 1910b, Sokolow 1911a). Several specimens of *R. hawaiiensis* sp. nov., were found with regenerating anterior and/or posterior ends (Figs. 7A–F). Worm fragments as small as four chaetigers seem to be capable of regenerating a whole worm. These regenerating fragments most likely belong to midbody chaetigers due to the enlarged digestive tube seen through the transparent body wall. If the anterior and poste-

rior ends begin regeneration simultaneously, the posterior end appears to regenerate faster than in the anterior end as there are a greater number of posterior segments. This could be due to the increment of new segments from the growing zone in the newly regenerated pygidium. Further experimental studies are necessary to fully understand the process of regeneration in this species.

Etymology. This species is named after the type locality.

Distribution. Known from shallow subtidal to 66 m off south shore of Oahu Island, Hawaii; on shallow reefs they inhabit the invasive algae *Gracilaria salicornia* and *Avrainvillea amadelpha*.

Remarks. Raphidrilus hawaiiensis **sp. nov.**, differs from R. harperi **sp. nov.**, and R. nemasoma by the presence of numerous bar–like papillae in the ventral proboscis, one or two dorsally biannulated achaetous segment between peristomium and chaetiger 1, and digestive tube clearly divided in three parts with a bottle–neck from chaetiger 4 to 5. The shape and arrangement of fibrils along the capillary chaetal blades in R. hawaiiensis **sp. nov.**, is very similar to R. harperi **sp. nov.**, by being thicker and having less space in between the fibrils in comparison with R. nemasoma.

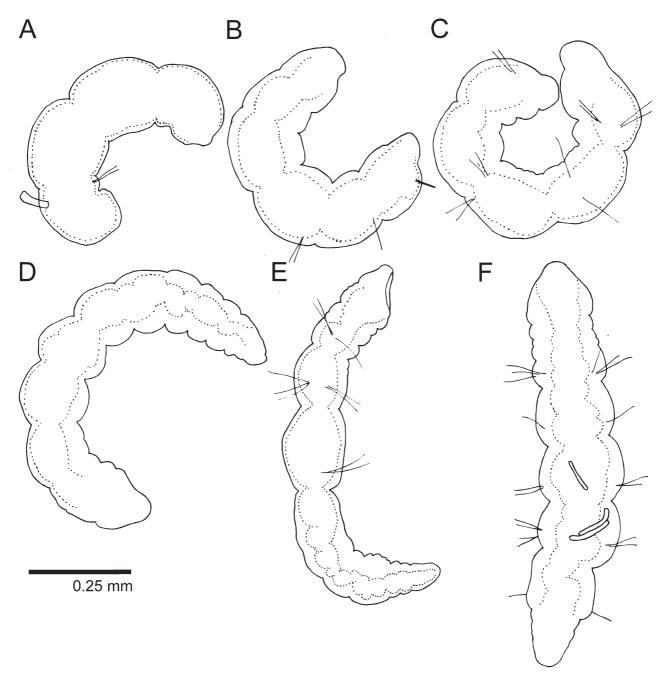


FIGURE 7. Six distinct individuals of *Raphidrilus hawaiiensis* sp. nov. in different stages of regeneration.

Discussion

The genus *Raphidrilus* was erected by Monticelli (1910a) and soon afterward, a very detailed study on the internal anatomy and reproduction of *R. nemasoma* was published by the same author (Monticelli 1910b). A year later, Sokolow (1911a) described *Ctenodrilus branchiatus* Sokolow, 1911 and also presented details of the internal anatomy and reproduction, but his new species was later synonimized with *R. nemasoma* in Sokolow (1911b).

Petersen and George (1991), by describing a new *Raricirrus* species, drew attention to the genus *Raphidrilus* and revised some erroneous records referred to *R. nemasoma*, which might actually belong to the Cirratulidae (i.e. Banse 1959b, Harris 1971), although the specimen illustrated in Banse (1959b, p. 170–171, fig. 2) does appear to be a juvenile of *Raphidrilus*. Thus, at that time, three distinct *Raphidrilus* species were known: *R. nemasoma* from the Mediterranean and two undescribed forms from Florida and British Columbia. *Raphidrilus harperi* sp. nov., from Florida is most likely the same species referred to by Petersen and George (1991) and the first one of the genus described from the Atlantic Ocean. In addition to the Mediterranean and Atlantic forms, two species, *R. hawaiiensis* sp. nov., and *Raphidrilus* sp. sensu Qian and Chia (1989) inhabit northwestern and northeastern Pacific waters, respectively.

Some authors, mostly based on the detailed studies available of *Raphidrilus* (Monticelli 1910b, Sokolow 1911a, Qian & Chia 1989), have regarded the peristomium in ctenodrilids as a complete ring positioned anteriorly to the first chaetiger (Rouse & Pleijel 2001) or as limited to the buccal region (Rouse & Fauchald 1997). However, the peristomium in *Raphidrilus* is actually a single annulus not easily distinct dorsally from the prostomium and precedes at least one truly achaetous segment. The dorsally biannulated achaetous segments are the unifying characteristics of all three described *Raphidrilus* species and it might be a consistent synapomorphy for this genus, but a careful examination of the undescribed species from British Columbia is needed.

The shape of the prostomium and peristomium, presence of sensorial cilia on the prostomium in addition to the oval nuchal organs, shape and presence of sub–annulations on abdominal segments, position and extent of the heart body, number, length and arrangement of capillaries on thoracic and abdominal regions, details of the fibril's insertion point on the capillary chaetal blades, position of anal aperture and presence of fields of cilia are all of specific value (Table 2). The presence of scattered sensorial cilia on the prostomium in addition to the oval nuchal organs is unique in juveniles of the undescribed species by Qian and Chia (1989) but it is uncertain if the adults also have these sensory structures.

The shape of the abdominal segments exhibits variability among the *Raphidrilus* species. *R. harperi* sp. nov., has abdominal segments 1.5–4 times longer than wide, *R. hawaiiensis* sp. nov., has abdominal segments as long as wide, sometimes sub–moniliform, and both *R. nemasoma* and *Raphidrilus* sp. sensu Qian and Chia (1989) have the abdominal segments twice longer than wide (Table 2). However, the shape of the abdominal region of preserved specimens might be a result of preservation artifacts and not truly species–specific.

Details of the capillary fibrils seen under SEM may represent a useful taxonomic character but this needs further investigation and refinement. For instance, we distinguished the serrated capillaries in relation to the gap formed by the insertion point between two longitudinal fibrils on the capillary chaetal blades. The longitudinal gap between two capillary fibrils is smaller in *R. harperi* sp. nov., and *R. hawaiiensis* sp. nov., in comparison to *R. nemasoma*.

The external morphology of the three nominal *Raphidrilus* species is very similar and the distinction among them is most accurate with the aid of a SEM. The arrangement of the anterior end in *Raphidrilus* is unique among the Ctenodrilidae but very similar among species. The shape of the prostomium, peristomium and first achaetous segment is very similar and the distinctions seen (e.g. one specimen of *R. hawaiiensis* **sp. nov.**, had 3 achaetous segments) might be due to unusual forms produced by asexual reproduction. Future genetic studies are necessary to complement this taxonomic evaluation and also to understand the phylogenetic position of *Raphidrilus* within the Ctenodrilidae.

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